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THE FACTORS THAT DETERMINE REGENERATION IN ANTENNULARIA.

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THE following experiments were carried out at the Naples Zoölogical Station during June and July, 1900. As there may be no opportunity in the immediate future of completing the observations, I have determined to publish them as they stand, in the hope that the results may stimulate some one, so situated as to obtain the necessary material, to take up the questions here raised and to bring them to a more satisfactory conclusion.

Loeb's experiments on Antennularia, made in 1892, show that pieces of the stem suspended in sea water always regenerate roots at the lower end and a new stem at the upper end. The result was the same whether the apical or the basal end of the piece was uppermost, *i.e.*, whether the piece had a normal or a reversed orientation. Similar results were obtained when pieces were suspended obliquely, the high end producing always the new stem and the low the new roots, etc. These results are similar to certain results that have been obtained in plants, although Vöchting has shown conclusively in many forms that the polarity of the piece is a much stronger factor in determining the regeneration than is gravity. Loeb drew the natural inference from his results, *viz.*, that gravity determines the kind of regeneration that takes place at the ends of the piece. Driesch,[1] who examined later the regeneration of Antennularia, found that when a piece of the stem is so placed "that its basal end is freely surrounded by water," a large number of roots are formed from that end. If the end with its roots is cut off, there is generally formed from the cut end a few new roots, but also always a more or less delicate stem composed of a few tubes. This stem is negatively geotropic.

[1] Driesch, H. Studien über das Regulationsvermögen der Organismen, I. *Roux's Archiv.* Bd. v, p. 383.

If the same end is again cut off, there develops rarely one or a few roots, but generally two or three vigorous stems. If the operation is repeated a fourth time, one or two stems are without exception produced.

There is no statement made by Driesch as to how these pieces were orientated with regard to gravity, but the results show that another factor than gravity has an influence on the regeneration. Unfortunately nothing is said with regard to what has taken place at the other end of the piece. I shall try to show that it is not improbable that this may be also a factor in the result, and if so it is possible that Driesch's results are due to this rather than to the action of the water on the free basal end, or at least both factors may be present.

My experiments were primarily undertaken in order to see how pieces would behave when fixed to a revolving wheel, but on account of the apparent disagreement between Loeb's and Driesch's results, it was first necessary to repeat the experiment of suspending pieces with two cut ends in order to see how far gravity acted upon them. In one series of experiments pieces were suspended in an aquarium by means of a silk thread. Some of these had the apical end upwards, others the basal end upwards, and still others were suspended horizontally. In nearly all cases roots developed in the course of a few days from both ends. If the ends were cut off, new roots developed again on both ends; although in one or two cases in which the apical end was uppermost a stem developed at that end. The pieces were from 3 to 5 cm. long.

By means of another device the experiment can be much more satisfactorily carried out. A small square piece was cut from a sheet of cork and a hole bored in its middle. The end of a glass rod, about 20 cm. long or longer, was pushed through the hole in the cork. If the piece of cork is neither too large nor too small, the glass rod, when put into an aquarium, will sink to the bottom until one end touches, but the other end will be held up in a vertical position owing to the buoyancy of the cork.

Pieces of the stem of Antennularia were fastened to the sides of the cork by means of two dried cactus spines, that were crossed over the stem and stuck into the cork.

In these experiments, made with pieces of different lengths, and from different parts of the old stem, the results were the same as before. In nearly every case roots developed from both ends, and even after these ends had been once removed. The experiments extended over two or three weeks. Whether, if continued longer, a stem would develop at the upper end among the roots there present, I do not know, but the results suffice to show that the most characteristic thing that occurs is the production of roots from both ends.

I was, therefore, not a little surprised to find in another series of experiments that a different result occurred. I placed in an aquarium a number of pieces of Antennularia that remained attached to the stones on which they had been found growing. Most of the pieces stood up vertically from the floor of the aquarium with the apical end upwards; a few pieces I suspended in an inverted position, *i.e.*, with the apical end downwards and the attached basal end upwards. In the former cases the apical ends did not produce roots at all, but a new stem. In the latter cases, in which the pieces were inverted, the apical end produced neither roots nor stem. Although these pieces were observed for only ten days, the time is ample to show that the pieces behave differently from pieces with two cut ends. I regret that I could not carry these experiments further.

One other result should be described, since it seems to have a direct bearing on the last experiment. In one case a very small piece had sunk to the bottom of a dish of water, where it stood with its basal end in contact with the glass. It lay there undisturbed, and attached itself at its basal end by means of new roots. *The apical end produced a shoot.* This result, taken in connection with the preceding experiment, seems to indicate that the development, or the presence of roots on the basal end, prevents the development of roots on the apical end. This result, if it prove constant, opens the way for several interesting experiments that so obviously suggest themselves as to require no further mention.

A few experiments were made with a rotating wheel constructed for the purpose. The wheel consisted of two parallel

rings of wire between which, at equidistant points, were sixteen paddles (5 cm. × 8 cm.) made of oblong pieces of sheet-copper; spokes (13 cm. long) attached the rings to an axis that rotated in two sockets. When the wheel was immersed in the water of an aquarium, and a stream of water from the tap was made to play (beneath the water) on the plates, the wheel slowly revolved, making about five and one-half revolutions in a minute.[1]

Pieces of Antennularia were attached to the wheel in the following way. Sheets of cork of the same size as the copper plates were attached to the underside of the latter by wire or string. Pieces of the hydroid were fixed to the cork in different positions by means of crossed cactus spines. The pieces were, on an average, about 15 cm. from the axis of rotation. The results were entirely negative. None of the pieces produced either roots or stems; and the pieces died sooner than did those in other experiments. As this experiment was carried out in a different aquarium, I cannot be certain that the death of the pieces was not due to other causes than to the rotation. Furthermore, it is not evident from the experiment whether the rubbing of the moving ends against the water suppressed the regeneration, or whether the result is due to the continuous change of position in regard to gravity. The rotation was too slow for the action of the centrifugal force to have played any important part. Since other experiments have shown that roots may develop at both ends of a piece suspended vertically, it is improbable that in the rotating pieces the changing position in regard to the action of gravity can account for the result, and it is much more probable that the motion of the piece through the water interfered with the regeneration at the ends. The experiment needs to be repeated more often, and other check experiments carried out in the same tank.

The work that I have done on the regeneration of Antennularia, while incomplete in many ways, shows at least that other factors than gravity enter into the result. I do not question the main part of Loeb's results, for they seem to show that gravity

[1] This wheel was left at the Naples Station in the hope that it might be used by some one to continue the experiments.

is a factor in the regeneration of this form ; but the development of roots at both ends that first takes place, as I have found, but which Loeb did not observe, and the behavior of pieces attached at one end, as described in the preceding pages, show that the factors determining regeneration are more involved than previous results seem to indicate.

BRYN MAWR COLLEGE, Feb. 4, 1901.